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Kenneth D. Rose
Johns Hopkins University School of Medicine, kdrose@jhmi.edu

Thomas M. Bown
U.S. Geological Survey

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Evolution

Additional fossil evidence on the differentiation of the earliest euprimates

(Omomyidae/Adapidae/*Steinius*/primate evolution)

KENNETH D. ROSE* AND THOMAS M. BOWN†

*Department of Cell Biology and Anatomy, The Johns Hopkins University School of Medicine, Baltimore, MD 21205; and †U.S. Geological Survey, Paleontology and Stratigraphy Branch, Denver, CO 80225

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ABSTRACT **Several well-preserved jaws of the rare North American omomyid primate *Steinius vespertinus*, including the first known antemolar dentitions, have been discovered in 1989 and 1990 in the early Eocene Willwood Formation of the Bighorn Basin, Wyoming. They indicate that its dental formula is as primitive as those in early Eocene *Donrussellia* (Adapidae) and *Teilhardina* (Omomyidae)—widely considered to be the most primitive known euprimates—and that in various dental characters *Steinius* is as primitive or more so than *Teilhardina*. Therefore, despite its occurrence at least 2 million years later than *Teilhardina*, *S. vespertinus* is the most primitive known omomyid and one of the most primitive known euprimates. Its primitive morphology further diminishes the dental distinctions between Omomyidae and Adapidae at the beginning of the euprimate radiation.**

Researchers are unanimous that the primate families Omomyidae and Adapidae represent the oldest and most primitive known "primates of modern aspect" (euprimates) (1–8), even though their precise relationships to living primates remain controversial. Although Plesiadapiformes may be related to Primates, their exclusion from the order is advocated by a growing number of authors (9–14), and there is general agreement that Euprimates is a holophyletic clade (3, 11, 12, 15, 16). Hence Omomyidae and Adapidae are probably the oldest known members of the order to which humans belong. The most ancient omomyids and adapids appear abruptly in the early Eocene of North America (earliest Wasatchian) and Europe (earliest Sparnacian) (7, 17–20), although an omomyid believed to be of late Paleocene age (Thanetian) has recently been reported from Morocco (21, 22).

Apart from the new Moroccan form, the oldest and most primitive unquestioned euprimates are the Euramerican omomyid *Teilhardina* (variously assigned to Omomyiformes or Tarsiiformes), the Euramerican adapid *Cantius*, and the European adapid *Donrussellia* (the last two assigned to either Adapiformes or Lemuriformes); all are widely considered to lie near the base of the Euprimates (4, 8, 18–20, 23–25). All three have a lower dental formula of 2-1-4-3, which is primitive for euprimates. Adapids generally differ from omomyids dentally in having small vertical incisors (also present in some omomyids), I_1 smaller than I_2; unreduced canine; four premolars, P_2 two-rooted, P_3 and P_4 narrow and elongate; and molar M_3 unreduced—most or all of which are believed to be primitive characters for Euprimates (4, 6). It is now known that the most primitive species of *Teilhardina*, *Teilhardina belgica* and *Teilhardina americana*, like primitive adapids, had small incisors (based on alveoli and known only for *T. belgica*), a moderately large canine, and four premolars (18, 20). No other omomyids (including more advanced *Teilhardina*) are known to have had four lower premolars. *Teilhardina* dental characters are derived compared with *Donrussellia* in having the lower canine and P_1 relatively more reduced, P_2 diminutive and one-rooted, P_3 and P_4 anteroposteriorly shorter, and M_3 reduced (18, 20, 26). Hence adapids are generally more primitive dentally than omomyids. The postcranial skeleton in the oldest euprimates is poorly known and character polarities are equivocal. The consensus seems to be that tarsal anatomy of early adapids is derived relative to that of omomyids (16, 27, 28), but some authors maintain that adapids are postcranially more primitive (18, 29).

Table 1. U.S. Geological Survey (USGS) samples

USGS no.	Description	Finder of sample
25026	Right dentary with P_4–M_3 and anterior alveoli	S. J. Senturia
25027	Right dentary with P_3–M_3	M. Shekelle
25028	Left dentary with P_3–P_4	J. J. Rose
28325	Left dentary with P_3–P_4 and anterior alveoli	H. H. Covert
28326	Left dentary with P_3–M_1	T. M. Bown
28466	Isolated right M_2	
28472	Isolated left M_1	
28473	Isolated right P_4	

Previously Unreported Material

Steinius vespertinus is a poorly known omomyid that has been known up to now solely from a few fragmentary lower and upper jaws from the early Eocene of Wyoming (20, 30, 31). Several new specimens were recovered from the lower Eocene Willwood Formation of the Bighorn Basin, Wyoming, during the summer field seasons of 1989 and 1990 (Table 1).

All but one of the specimens come from a small quarry at USGS fossil vertebrate locality D-1762; USGS 25028 is from D-1859 [both localities at the 414-m level of the Willwood Formation (32)].

These specimens preserve evidence of the lower antemolar dentition, including several features in which *S. vespertinus* is equally or more primitive than *T. belgica* and *T. americana* (Figs. 1–3): a relatively large canine alveolus; two premolar alveoli between P_3 and the canine; simple, uninflated, and elongate P_3 and P_4 (Table 2); P_3 relatively tall and unreduced; and P_4 with a distinct, low metaconid.

The alveoli of the incisors are preserved in USGS 25026 (Fig. 2). Although the lateral side of the dentary is broken away at the front, it is clear that I_1 was larger than I_2, and its alveolus is slightly larger than that for the canine. The

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Abbreviations: USGS, U.S. Geological Survey; I, incisor; P, premolar; M, molar.

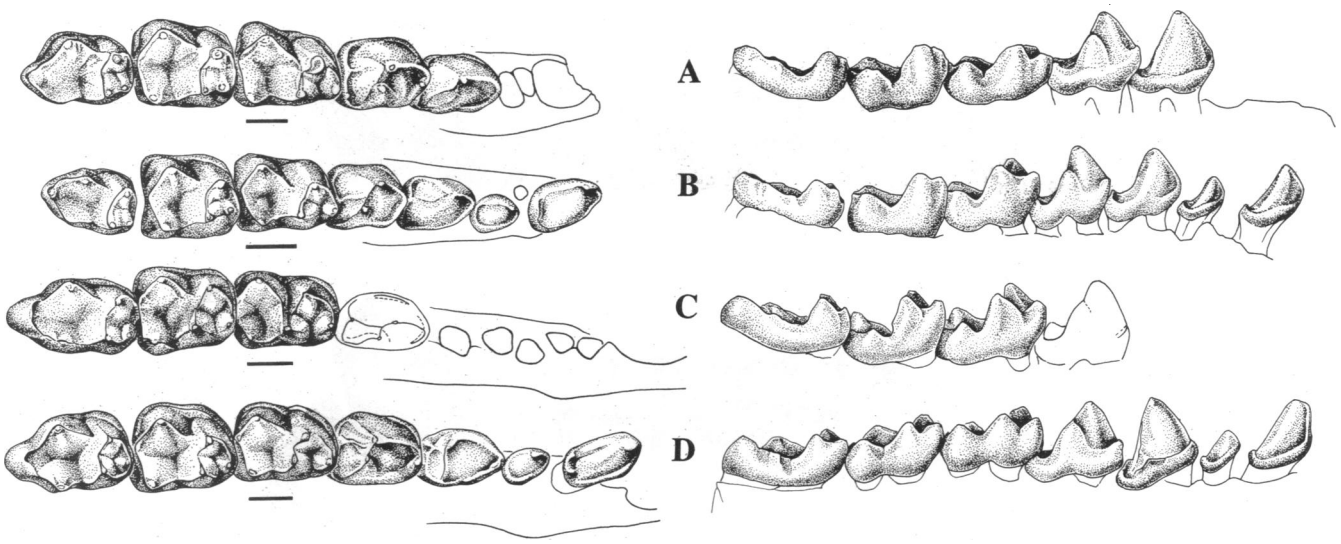

FIG. 1. Left lower dentitions of early euprimates in occlusal (*Left*) and lingual (*Right*) views. (*A*) *S. vespertinus*, showing P_3–M_3 and alveoli for canine, P_1, and P_2 [based on holotype (American Museum of Natural History 16835), USGS 28325, and USGS 28326]. (*B*) *T. americana* with canine and P_2–M_3 (holotype, University of Wyoming 6896; P_1 alveolus restored from University of Michigan nos. 75610 and 77391). (*C*) *Donrussellia provincialis* with M_1–M_3 (Muséum National d'Histoire Naturelle, Paris, RI 170); P_4 and anterior alveoli as reported by Godinot (19, 33). (*D*) *Omomys carteri* with canine, P_2–M_3 [based on Yale Peabody Museum nos. 11805 and 13209; C–P_3 as reported by Szalay (18)]. (Bars = 1 mm.)

alveolus tapers beneath the canine socket, and the dentary is shallower anteriorly; consequently, I_1 must have been comparatively smaller than in *Tetonius* or advanced *Teilhardina* (although apparently larger than in *T. belgica*). The alveolus for I_2 was displaced laterally relative to I_1 and the canine.

In analogy with *Teilhardina*, the anterior premolar alveoli of *Steinius* are interpreted to have held one-rooted P_1 and P_2 rather than a two-rooted P_2 and no P_1; hence, the lower dental formula was 2-1-4-3. This interpretation is favored because no early euprimate is known to have lost P_1 while retaining a two-rooted P_2; however, early adapids retained P_1 together with a two-rooted P_2. Judging from its alveolus, P_1 in *S. vespertinus* was relatively at least as large as or larger than that in *Teilhardina* and was also displaced laterally. In USGS 28325 the P_1 alveolus is approximately the same size as that for P_2, but most of the alveolus lies buccal to the median axis of the tooth row. P_1 in USGS 25026 appears to be smaller (Fig. 2), but this is probably an artifact of breakage of the lateral side of the dentary and not a true indication of the size of this tooth.

P_3 and P_4 are more elongate and less basally inflated than in *T. americana* or *Tetonius* (Figs. 1 and 3), closely approaching *T. belgica* in this regard. P_3 is simple, tall, and slightly

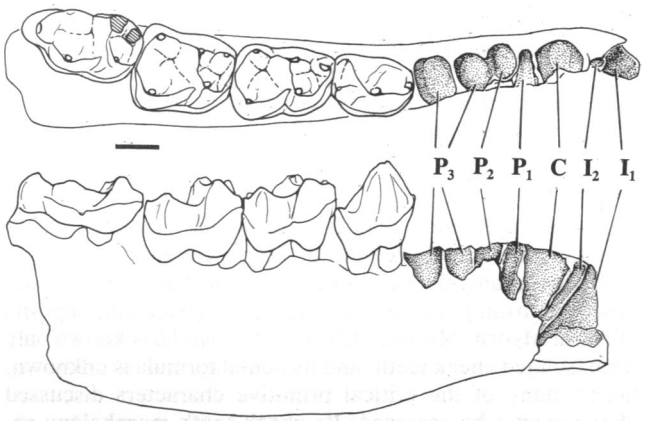

FIG. 2. *S. vespertinus*, USGS 25026, right dentary with P_4–M_3 and alveoli for all anterior teeth, in occlusal (*Upper*) and buccal (*Lower*) views. (Bar = 1 mm.)

larger relative to P_4 than in *Teilhardina*. P_4 has a small, low paraconid and a higher, more prominent metaconid; the latter is, however, relatively low, comparing closely with the metaconid elevation in *T. americana*.

Steinius also closely resembles the adapid *Donrussellia* in several of the primitive euprimate characters listed above (unreduced canine, presence of four premolars, uninflated and elongate P_{3-4}, P_4 with low metaconid) as well as in having relatively broad molar talonid basins with peripheral cusps and no basal inflation and a less reduced M_3 than in *Teilhardina*. Only in having a somewhat enlarged I_1 is *Steinius* apparently more derived than the most primitive *Teilhardina*. *Donrussellia* is more primitive than *Steinius* (and *Teilhardina*) in having narrower and more elongate P_{3-4} (Table 1), a two-rooted P_2, more acute molar cusps, and more separated molar paraconids and metaconids (especially on M_2).

Thus, *S. vespertinus* appears to be the most primitive known omomyid and, as such, it helps to clarify the polarity of dental characters in basal euprimates. Aforementioned traits held in common among all three genera can reasonably be taken as primitive euprimate characters, whereas those shared only by *Steinius* and *Teilhardina* are synapomorphic for Omomyidae. This interpretation of character polarities is substantiated by comparison with *Purgatorius*, the oldest plesiadapiform and the only one sufficiently primitive to be structurally ancestral to euprimates. The new specimens of *Steinius* also provide evidence of antemolar similarity to some Omomyinae, specifically Bridgerian *Omomys* (Fig. 1), thereby strengthening the probable phylogenetic link between these two genera and substantiating the status of *Steinius* as the most primitive known omomyine (31, 34).

Discussion

In the last decade or so, certain other recently discovered fossils have been proposed as the oldest and/or most primitive euprimate. *Altanius orlovi* (very early Eocene, Bumbanian, of Mongolia) was described as an anaptomorphine omomyid (35). Its cheek teeth also closely resemble those of certain plesiadapiforms (35, 36). *Altanius* is unequivocally very primitive, retaining four premolars, a two-rooted P_2, and unreduced canine and M_3 (35, 37). However, superimposed on this very plesiomorphic pattern are unusual derived characters

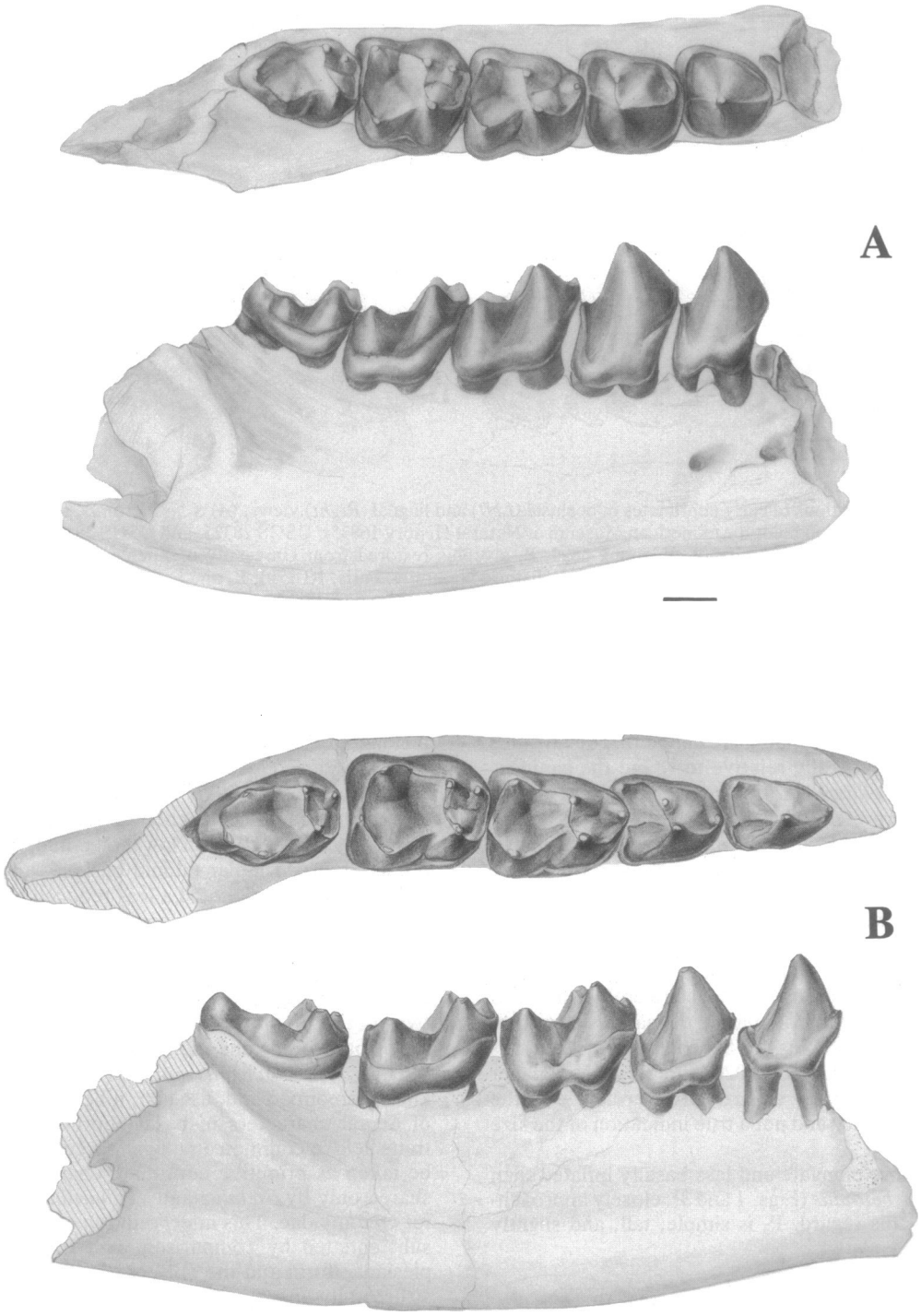

FIG. 3. (*A*) *Tetonius matthewi* , Yale Peabody Museum 35016, right dentary with P_3–M_3 in occlusal (*Upper*) and buccal (*Lower*) views. (reprinted with permission from ref. 20; copyright The Paleontological Society). (*B*) *S. vespertinus*, USGS 25027, right dentary with P_3–M_3, in occlusal and buccal views. Note relatively longer and narrower P_3 and P_4, larger M_3, and more peripheral molar cusps in *Steinius*. (Bar = 1 mm.)

(e.g., exodaenodonty, high lingual cusps, short molar talonids, broad and anteroposteriorly compressed P_{3-4}), which indicate that, whatever its affinities, *Altanius* belonged to a divergent clade of archaic origin. This unusual combination of characters removes *Altanius* from consideration as a stem omomyid.

Decoredon elongetus (middle Paleocene of China) was proposed as a euprimate (?omomyid) by Szalay and Li (38). The species is based on poorly preserved jaw fragments initially allocated to two different mammalian orders, Anagalida and Condylarthra (39, 40). Although the elongate P_4 (with distinct metaconid) and M_3 are reminiscent of the primitive euprimate condition, demonstrable evidence of primate affinities will require better specimens.

A new omomyid, *Altiatlasius koulchii*, has recently been described from putative late Paleocene (Thanetian) deposits of Adrar Mgorn, Morocco (21, 22). *A. koulchii* is known only from isolated cheek teeth, and its dental formula is unknown, hence many of the critical primitive characters discussed above cannot be assessed. Its cheek tooth morphology appears to be very primitive and has been compared with *Omomys*, *Donrussellia*, and *Cantius*, among others (21, 22); comparison with *Steinius* has not yet been possible. Although

Table 2. Mean dimensions of P_4 in some early euprimates

Species (sample size)	Length, mm	Width, mm	Length/width ratio	Ref.
Steinius vespertinus (n = 5)	2.03	1.55	1.31	This paper
Teilhardina belgica (n = 9)	1.54	1.18	1.31	20
Teilhardina americana (n = 18)	1.60	1.39	1.15	20
Tetonius matthewi (n = 72)	2.05	1.93	1.06	20
Donrussellia provincialis (n = 1)	2.20	1.50	1.47	19
Donrussellia magna (n = 1)	3.07	2.03	1.51	25
Cantius torresi (n = 1)	2.80	2.40	1.17	7
Cantius ralstoni (n = 32)	3.31	2.50	1.32	USGS coll.
Omomys carteri (n = 20)	2.19	1.59	1.38	18

coll., Collection.

its omomyid affinities and late Paleocene age remain to be corroborated, *Altiatlasius* may well be pertinent to the origin of Omomyidae; but more complete specimens are needed to evaluate this possibility.

Apart from *Donrussellia*, Euramerican *Cantius* is the most primitive adapid. Gingerich (7) suggested that the oldest species, *C. torresi* (basal Wasatchian of Wyoming), was even more primitive than *Donrussellia*, particularly in premolar morphology. But close correspondence among *Steinius*, primitive *Teilhardina*, and *Donrussellia* in premolar form and other characters discussed above, as well as the presence of several derived characters in *Cantius* (basally swollen cheek teeth, faint-to-pronounced crenulation of enamel, close apposition of paraconid–metaconid cusps on M_2 and M_3) indicate that *Donrussellia* lies closer to the euprimate morphotype than does *C. torresi* (25, 42).

Although adapids and omomyids have generally been placed in separate higher taxa of primates (e.g., suborders), the earliest members of each group are in fact very similar both dentally and postcranially—sufficiently so that diagnoses of these two families have been chronically vague, and confusion has surrounded the proper family assignment of such taxa as *Donrussellia* [*D. gallica*, the type species of *Donrussellia*, was initially allocated questionably to *Teilhardina* (41)] (6, 18). As our knowledge of the earliest euprimates has improved, the number of characters distinguishing adapids and omomyids has steadily declined, making separation of Omomyidae from Adapidae exceedingly difficult on dental characters alone (dentitions constitute by far the principal fossil remains for most early euprimates). In view of the primitive characteristics of *Steinius vespertinus*, there remains only one distinctive dental trait separating basal omomyids from primitive adapids: a one-rooted (vs. two-rooted) P_2. Thus these forms—*Donrussellia*, *Cantius*, *Teilhardina*, and *Steinius*—are unquestionably close to the euprimate dental morphotype and may well have shared a late Paleocene common ancestor, perhaps in Africa (21, 22). In fact, only primitive euprimate (dental) characters unite *Donrussellia* with Adapidae, and this genus appears to be dentally more nearly representative of the basal euprimate—the expected common ancestor of Omomyidae and Adapidae—than any other known form.

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